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Back to basics: sociometry and sociogenesis of ant societies (Hymenoptera: Formicidae)

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Abstract

For several decades, social insect research has been dominated by a "top-down" approach that begins with evolutionary theory or mathematical models. A "bottom-up" approach based on a detailed description of the physical, numerical and life history attributes of social insect colonies has been largely neglected. I define the quantitative description of colony attributes as sociometry, the measuring of a society. I argue that sociometry can be a generous, unbiased source of testable hypotheses, and leads to a deeper understanding of social insect function, life history and evolution. Whereas there is a large deficit in sociometric data, the deficit of colony ontogeny data, defined as sociogenesis, is even greater. Yet, social insects offer an opportunity to generalize developmental processes to the colony level. Moreover, these processes can be anchored in local ecological conditions, thus linking development to evolution. A simple, practical method for the simultaneous collection of sociometry / sociogenesis data is described. By complete sampling and measurement of the full size range of a focal species' colonies on several carefully chosen dates throughout the annual cycle, a description (sociometry) of colonies during growth (sociogenesis) and through the seasons (annual life cycle) is generated. Our understanding of social insect biology would be greatly enhanced by the widespread adoption of the sociometric / sociogenesis method as the starting point of social insect studies.

Key words: Colony growth, colony development, colony size, worker size, worker demography, colony ontogeny, colony evolution, sociogenic method, sociometric method, review, position paper.

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Introduction

Imagine that you were trying to determine why automobile No. 1 consumed more fuel per km than automobile No. 2, yet you did not know the engine type, the vehicle weight and dimensions, the age, nor the conditions under which each had been used. It seems unlikely that you could arrive at a credible answer to your question. Moreover, you would probably be wise to inquire about gear ratios, power-train characteristics, engine displacement and fuel / air mixture variation, as these are probably all functionally linked to your measure of interest. This all seems reasonable and logical, perhaps because an automobile is a machine engineered by humans, making it obvious that its performance is the product of its construction.

We can also think of a social insect colony as a machine, engineered not by humans, but by natural selection to produce an output (the factory-fortress is a popular metaphor). The machine metaphor emphasizes that social insect colonies, like cars, are composed of a number of parts that work together in particular ways to accomplish the colony's functions. Like cars, social insect colonies can be produced in a range of sizes, fuel-use rates and time-in-production, each appropriate to a particular context. It is unlikely that when you want to haul a trailer loaded with four horses, you would ignore the size of the car you intend to haul it with. Size matters.

Social insect colonies and their populations, like cars and their populations, also have collective properties that emerge from their individual attributes, attributes that in their turn are shaped by ecological and evolutionary, or in the case of cars, socioeconomic, engineering and political history. Collective properties, be they of colonies or populations, can be addressed from "the bottom up" through detailed description, pattern detection and experimental dissection, or from "the top down" from evolutionary theory and mathematical models. Each approach reveals phenomena not available to the other, and both are necessary for complete understanding, a point also made by SEELEY (1995). I cannot improve upon his words, so I present them here:

> The fundamental challenge … at all levels of biological organization is to explain the abilities of units at one level in terms of the actions and interactions of lower-level units. … If … one examines simply the exterior of a system, one is limited to measuring the inputs and outputs of the intact system and attempting to infer what goes on in between, the so-called top-down, black box, or phenomenological approach. One danger of looking only at the outside is that it is easy to overlook things inside, especially those whose effects on the system are weak. … A second and greater danger of the top-down approach is that it is exceedingly easy to err in one's attempts to deduce the bits and pieces of living machinery that implement a given system-level property. … The problem is that one's [mathematical] model of the inner workings may not correctly de-

> scribe them, even if its predictions fit some of the facts. … [H]ence the top-down approach is likely to lead to a falsely simplified view of the phenomena of life. … Thus looking at a system from the top down helps us to see what the questions are, while looking from the bottom up enables us to see the answers.

While the widespread practice of the top-down approach in many areas of social insect biology has produced important insights, its dominance, sadly, has largely crowded out the alternate bottom-up approach that begins with a description of ants and colonies and asks how higher-level properties and evolutionary patterns arise from them. The current fashion is particularly perplexing because description and pattern recognition have always been a rich and generous source of testable hypotheses. It has been thus for most of the history of biology. Sociometry (defined below) simply applies this hoary approach to the study of social insects.

The purpose of this essay is three-fold: (1) to convince the reader that there is much gold to be discovered through the bottom-up study of social insect biology; (2) to suggest, as SEELEY (1995) has, that the top-down approach can easily lead to erroneous explanations or miss alternate hypotheses, and (3) to provide interested parties with a simple method for collecting this bottom-up information for ant colonies.

Sociometry

By sociometry, I mean the quantitative measurement and description of all parts of an insect society, preferably throughout its annual cycle. How many workers, queens, larvae and pupae are there? How large and variable are each of these, and how much energy does each contain? Colony age, age and size at first reproduction, worker and sexual production rates and life spans, sizes and energy content of sexuals, seasonal changes in various measures and many other attributes as described in TSCHINKEL (1991). In large measure, my notion of sociometry is similar to that of "character and character state" of STEINER & al. (2009).

Generally, we seem to accept the notion that in order to understand how a machine does what it does, we must know its construction and how the parts relate to one another, and we accept as a given that the possible combination of parts is limited. We also accept that the machine is at least the sum of all its parts and interactions and cannot be understood one part at a time. Having gained such understanding, we can generate testable hypotheses concerning how the machine or the colony works, and how changes in the parts and their relationships affect higher level outcomes, be they gas mileage, metabolic rates, horsepower or sexual production. This is daily fare for every car mechanic. Strangely, when it comes to studying social insects (at least ants), we ignore what we found so obvious in the engineering world. Hundreds of papers are published every year in which the authors have little knowledge of the basic construction or size of their machine, the social insect colony, or superorganism.

Authors concern themselves with intricate questions about genetics, division of labor, evolution of castes, and many other sophisticated subjects, yet rarely know (or at least publish) such basic superorganismal traits (that is, sociometric data) as colony size, colony age, worker size distribution, queen size and age, size (or age) at first reproduction, seasonal cycles and many others. Knowledge of these attributes is important, because many of them are linked to each other in such a way that they evolve together, and changes in one are accompanied by changes in one or several others (i.e., syndromes). We often discuss the evolution of selected superorganismal traits as though they could evolve independently of each other, as though the engine displacement could change independently of torque at the drive wheels, but as with car parts, the possible combinations are limited. Much of social insect research addresses the ultimate, evolutionary level (e.g., kinship selection) and rarely the proximate mechanisms, even though the latter might lead to alternate explanations. In line with my arguments, STEINER & al. (2009) point out, "evolutionary concepts have developed more rapidly than life history data could be collected for validation."

Appreciation of this linkage is particularly important in comparative studies, when authors wish to argue for certain patterns of change in selected superorganismal characters during the evolution of a taxon. Linkage of such traits to others must be understood for meaningful interpretation of such comparative studies. Imagine that you are studying foraging by several species within your favorite genus of ants, and discover that workers of species A on your baits are smaller than those of species B, and that B usually displaces A from the baits, or maybe chooses larger prey. You write a long, erudite paper in which you argue that B evolved larger workers as the result of competition with A. You even get this paper published.

However, had you done a proper sociometric study, along with a bit of natural history, you would have opened the door to several other, more interesting interpretations. You would have discovered that, compared to species A, the queens of species B start new colonies in situations leading to higher mortality during the founding stage. Species B has thus been selected to produce more alates to overcome this juvenile mortality, and has accomplished this by evolving larger mature colony size, therefore producing more alates. B's larger colony size is the outcome of the delay of metamorphosis in worker larvae so that worker adult size has increased, which in turn has lead to a lower metabolic rate, longer worker lifespan and lower worker turnover, leading directly to B's larger colony size.

An alternate path to larger colony size might have been for the queen to boost her egg-laying rate by evolving more ovarioles, leading to larger mature colony size. Worker mean size increases with colony size (a rule that does not change within the genus), so that when colonies of species B reach their maximum size, their workers are, on average, larger than those of species A simply because their colonies are larger (many of these patterns are actually present in the species of fire ants, TSCHINKEL 2006). There are probably more links less directly relevant to the question in hand: Larger colony size probably means larger foraging areas, lower per-mg metabolic rate, larger queen-worker dimorphism, longer colony life span, greater spermathecal sperm storage, greater age at first reproduction and longer growth periods.

My 1991 paper (TSCHINKEL 1991) made many of these points in some detail, but little has changed since then. Other than a handful of papers, most by myself and my students, social insect researchers have (sadly) not responded to my clarion call. As a result, we still do not know the major sociometric attributes of even the most popular research species. To be fair, scattered sociometric data appear in many papers, but usually only as an incidental product of some other study. Gleaning these data from the literature is a daunting task fraught with many issues of data quality and uniformity of collection methods. Few authors set out with the goal of producing a comprehensive, quantitative description of an insect society. Few authors seem even to recognize that there is value in such a humble undertaking. As a result, a rich source of testable hypotheses and evolutionary insight is neglected.

A perceptive reviewer of this manuscript made the point that while collecting such data would be good, in real life biologists grapple with the question, "Given my hypotheses and budget, how do I allocate time and effort toward answering an interesting question?" In other words, how much do I gain by investing considerable time and energy toward collecting the sociometric data? I believe this point represents the currently popular attitude that all biological research should be engaged in "hypothesis testing." I have addressed this issue above by contrasting the top-down vs. bottom-up approaches. Darwin would never have come to his deductions had he not spent years accumulating descriptive data on patterns. Initially, he tested no hypotheses, but once he saw broad and detailed patterns, hypotheses flowed like water, and still do. I am grateful to this reviewer for making his or her point, because it clarifies what I believe the value of the sociometric / sociogenic method to be – in establishing a detailed description of the composition and development of social insect colonies, multiple hypotheses concerning cause / effect and evolution will flow, stimulating fruitful, well-grounded and insightful research. As an example, I offer my work on fire ants (TSCHINKEL 1993; summarized in TSCHINKEL 2006). The initial aim of this work was description and pattern recognition, but the outcome fairly bristles with testable hypotheses, many of which would not have arisen *a priori*.

The same reviewer also asked if lack of sociometric data has led to "gross errors" of interpretation. Unfortunately, this question can only be answered with sociometric data, and these are generally not available. Fire ant sociometry suggests that such errors are possible, as described above in the worker-size example.

Sociogenesis (colony ontogeny)

This brings us to my second theme, colony ontogeny. Obviously, sociometric attributes do not spring whole from the brow of Zeus. Rather, they are the product of colony (or superorganism) ontogeny from founding to maturity, a process WILSON (1985) called "sociogenesis." If the deficit of sociometric data is great, that of sociogenic understanding is even greater. WILSON (1985) and TSCHINKEL (1993, 1998, 1999, SMITH & TSCHINKEL 2006) showed that the changes during sociogenesis are profound. The mature superorganism is as different from its founding stages as the mature vertebrate is from the early embryo. This means that knowledge of the chosen superorganism's size and the stage of ontogeny is important. As superorganisms, social insect colonies develop from founding to maturity in a manner analogous to the development of a non-social organism. Just as the organism develops from the zygote to the adult through the rules and interactions of ontogenesis, so the superorganism develops from the founding condition to maturity through the rules and interactions of sociogenesis. Just as differences among species of singular organisms are the result of differences in their ontogenesis, so are differences among species of superorganisms the result of differences in their sociogenesis. Understanding the evolution of superorganisms requires knowledge of sociogenesis, just as understanding the evolution of organisms requires an understanding of ontogenesis.

That the study of ontogenesis in all its complexity and glory has produced impressive insights is beyond doubt (CARROLL 2005). That sociogenesis has, unfortunately, been largely unrecognized as a promising field of study is also beyond doubt. Perhaps this is in part because of a prevailing impression that the only thing that changes as the superorganism grows is the number of workers, with maybe some sexuals thrown in later. Yet this is demonstrably not true, as has been well-documented in a small number of cases (BRIAN 1957, PLATEAUX 1980, WOOD & TSCHINKEL 1981, KITAMURA 1984, WILSON 1985, FOWLER 1986, PLATEAUX 1986, GIBSON 1987, ITO & al. 1988, CASEVITZ-WEULERSSE 1991, TSCHINKEL 1993, 1998, 1999). For example, the incipient fire ant colony containing a few workers is quite different from its mature counterpart containing 300,000 workers. As the former grows into the latter, mean worker size quadruples, percent major workers increases from none to about 35%, mean worker lifespan increases greatly, worker turnover decreases from 600% per annum to about 300%, percent fat stored in workers increases greatly, especially in the largest workers, the mix of available labor shifts greatly, the worker / brood ratio increases greatly, queen weight triples, and her egg-laying rate increases by orders of magnitude. Beyond a size threshold, the colony produces sexuals in approximate proportion to its size. Although few other studies have been so comprehensive, several have documented an increase in worker size with colony size.

Recently, YANG (2007) has argued eloquently that the superorganism offers an exciting opportunity to generalize developmental processes beyond the early embryonic stages of unitary organisms. My arguments tie in nicely with his thinking, and I recommend his paper to readers. My approach to sociogenesis is rather practical – how can we get the data, and how should we interpret them? I will get to this in the next section. YANG (2007) offers a more philosophical, profound view of the developing superorganism, arguing that many of the general processes and interactions that build the developing organism also operate in the developing superorganism. Examples include homeostatic regulation, activation / inhibition, ontogenetic differentiation, reaction norms, and positive and negative feedback.

YANG (2007) points out that the current EvoDevo approach and model organisms rarely address natural selection, i.e., "how developmental, homeostatic and adaptive processes operate in evolution." Instead, the focus is on proximate mechanisms in a non-evolutionary context. Using social insect colonies as a model developing system would allow developmental mechanisms and outcomes to be seen in an evolutionary context because social insects usually display large geographic variation within populations because natural selection has adapted them to local conditions. Yang's work on geographic variation of the worker caste of *Pheidole morrisi* presents an example (YANG 2006). Variation in sociogenesis and its outcome is the direct effect of local natural selection across the geographic range of a species. Enlarging the scope of EvoDevo to superorganisms will illuminate how critical developmental principles, processes and interactions extend beyond the individual. Moreover, studying developmental mechanisms of the superorganism in an ecological context addresses core issues of life history evolution in social insects. If we are to engage in this important question, we must begin with a description of the sociogenesis of our study species.

OSTER & WILSON (1978) elaborated the theory of adaptive demography, the idea that the schedules of births, body size, age-related changes and deaths of the individuals making up social insect colonies are adaptive at the colony level, responding to natural selection (see also BRIAN & ELMES 1974, CAMMAERTS 1977, BERNSTEIN 1984, RISSING 1987, SCHMID-HEMPEL 1992). Adaptive demography shapes the allocation of labor to various colony functions. The theory is explicitly developmental, inviting investigation of how the ontogenetic patterns and interactions of the individuals making up the colony are expressed in the observed adaptive demography, which is in turn, a colony level adaptation. Adaptive demography allows us to connect local ecological conditions to evolution through sociogenesis.

Ecological issues – size matters

Imagine that you are an ecologist interested in the role ant species play in, say, a grassland community. If you followed typical procedures, you might pitfall trap or Winkler-extract the ants and report their abundance and richness. If you were very dedicated and hip, you might try to count the number of colonies. It is unlikely that you would estimate colony size or probably even worker size. Yet, these two attributes are key ecological characters, and are related to one another. For example, in the fire ant, *Solenopsis invicta*, mean worker size quadruples between founding and maturity, territory size increases in proportion to spring colony biomass, and forager density decreases more than 80% in the spring (but not the fall). Colony size variation and distribution therefore has a large effect on the landscape-scale density and mean size of foragers (TSCHINKEL 2006). Clearly, a correct interpretation of *S. invicta*'s role and impact in its community requires knowledge of these (and other) sociometric variables.

Body size is generally accepted as an attribute of central importance. It is related to a host of ecological and physiological variables, ranging from metabolic rate to life span and home-range size. No ecologist or physiologist would fail to take note of the body size of a unitary study animal. Yet social insect biologists largely ignore colony size, the "body size" of the superorganism, as a variable of importance.

Getting practical: the sociometric / sociogenic method

Nevertheless, the small number of sociometric-sociogenic papers that appeared since 1991 allows me to make two points. (1) A great deal of ant research, especially ecological and natural history studies, suffers from not being founded on a firm knowledge of the sociometry and sociogenesis of the species involved; (2) Getting such data, while perhaps not fashionable, is not difficult, and the methods for doing so are simple and cheap.

Through a simple procedure, it is possible to collect a large number of sociometric data while relating these to both the seasonal cycle and colony size. In addition to producing many important attributes of the colony and its inhabitants, the procedure yields a picture of how these attributes change in relation to colony size and the changing seasons, i.e., the annual and the life cycles, both of which are key adaptive traits cued to the local ecology (sociometric attributes are usually not strongly related to age because age and size are largely uncoupled). Moreover, these descriptions generate many testable hypotheses.

Here is how it works – on several well-chosen dates throughout the year, the investigator collects a number of ant colonies in their entirety, choosing the colonies so that all colony sizes, from largest to smallest are represented. If that means digging a lot of deep holes (TSCHINKEL 1987, 1998, 1999), well, shovels are cheap, and most of us can use the exercise.

For the truly ambitious, it is also possible to stratify the collection of the colonies, keeping captures from different depth levels separate. The well-known movement of workers away from the brood area as they age actually takes place in a vertically-organized nest and is an integral part of colony life history, but this has been described in nature only a few times (e.g., KONDOH 1968a, b, MACKAY 1981, PORTER & JORGENSEN 1981, TSCHINKEL 1987, 1998, 1999). For the still more ambitious, it may be possible to describe the nest architecture in relation to depth.

Recently, I have used a wax-casting method that greatly improves capture of entire colonies, and captures every ant in the place where it stood or lay at the time of casting. The method is simple (TSCHINKEL in press): One melts paraffin over a propane camp stove, taking care not to heat the paraffin over 100°C, and then pours this paraffin into the entrance of the ant nest. Results are improved by wet soil. When the paraffin has hardened, one excavates the cast (by levels, if desired), re-melts it, and recovers the ants (and any other nest contents) intact. Residual paraffin can be removed by absorption into tissue or clean-up with organic solvents. It remains to be determined whether these ants will still give reliable fat content data, but this is a technical detail that can be worked out. With careful excavation, one renders the nest's architecture in the bargain (reconstruction from pieces will usually be required), and determines the spatial distribution of all the ants within the nest. There is convincing evidence that spatial distribution is a functional part of colony social structure (MACKAY 1981, TSCHINKEL 1987, 1999), related as it is to division of labor and worker age.

Analysis of the data is straightforward, too. Having completed the collection of the nests, the investigator has in hand the complete nest contents for the full range of colony sizes available on several dates (minimum, four) throughout the seasonal cycle. Each nest sample may also be stratified by vertical location (e.g., top third, middle third, bottom third). Contents of each sample are then separated by type and counted (e.g., adult workers, pupae, larvae, male alates, female alates, male pupae, female pupae, sexual larvae, queen(s)), and the size and dry weight of each of these is determined. In polymorphic species, workers would probably be stratified into several size classes. Determination of fat content (by weight loss upon extraction) allows energetic estimates to be made. Additional measurements might include dimensions of workers and alates, counts of callows, estimates of the pigmentation stage of pupae. None of this requires expensive equipment or difficult procedures.

The descriptive statistics and regressions derived from these counts and measurements would then paint a picture of the actual range of colony sizes found in the sampled habitat, and how colonies change during growth (sociogenesis: regression vs. colony size) and through the seasons (seasonal life history: analysis of variance by collection date). A little more effort can yield other important information: Determination of the temperature regime at several depths in typical nests throughout the year, and the rate of pupal development in relation to temperature combined with the pupal censuses by depth allow fairly realistic birth rates to be calculated. Because of the nature of the sampling regime, birth rates can then be related to both colony size and season. The proportion of callow workers gives a crude estimate of worker age distribution. Estimates of worker longevity in relation to temperature, however crude, allow the calculation of worker turnover. Application of the fat content allows the calculation of energy distribution among alates, workers of different size and age (callows vs. dark workers), and various types of brood. Fat storage is a crucial part of the seasonal cycle and alate production in most ants (TSCHINKEL 1993, 1999).

Upon completion, the investigator will have a greatly enhanced understanding of his or her subject species, including an understanding of the profound changes occurring during sociogenesis and through the seasons. True, the method relates sociometric variables to colony size, not to age, but in most social insects, colony size is probably more important than age. For example, in *S. invicta*, colony size is poorly correlated with colony age by the time colonies are one year old, and colony characteristics are mostly correlated to colony size (TSCHINKEL 2006), and this is probably typical of ants in general (WILSON 1985, HÖLLDOBLER & WILSON 2009). He or she can then reason from a basis of knowledge.

Based on this picture of the superorganismal life and seasonal cycle, the ecologist can then compute realistic population models after determining the colony size distributions in natural populations. Such models would implicitly recognize the superorganismal nature of social insect colonies, each with characteristic size and size-associated attributes, each at a characteristic stage of sociogenesis and seasonal cycle.

True intuitive knowledge of social insects can come only from great familiarity with the intimate details of their physical makeup and their life histories. The sociometric / sociogenic method offers a tool to gain a substantial part of this knowledge. It is time to pick up this tool and get to work.

Zusammenfassung

In den letzten Jahrzehnten wurde die Forschung an sozialen Insekten von einem "Top-Down"-Ansatz dominiert, der mit Evolutionstheorie oder mathematischen Modellen beginnt. Ein "Bottom-Up"-Ansatz, der auf der detaillierten Beschreibung der physischen, numerischen und lebensgeschichtlichen Eigenschaften einer Kolonie sozialer Insekten basiert, wurde kaum gewählt. Ich definiere hier die quantitative Beschreibung von Kolonieeigenschaften als Soziometrie, also das Vermessen einer Sozietät. Ich argumentiere, dass Soziometrie eine ergiebige, nicht verzerrende Quelle testbarer Hypothesen sein kann, und zu einem tieferen mechanistischen, lebensgeschichtlichen und evolutionsbiologischen Verständnis sozialer Insekten führt. Während es also ein großes Defizit an soziometrischen Daten gibt, ist das Defizit von Daten zur Ontogenese einer Kolonie, definiert als Soziogenese, sogar noch größer. Dennoch bieten soziale Insekten Möglichkeiten zur Generalisierung von Entwicklungsprozessen auf dem Niveau der Kolonie. Darüber hinaus können diese Prozesse mit lokalen ökologischen Bedingungen in Beziehung gesetzt werden, wodurch ein Bindeglied zwischen Entwicklung und Evolution hergestellt wird. Eine simple, praktikable Methode zur zeitgleichen Erfassung von Daten zu Soziometrie und Soziogenese wird vorgestellt. Durch das komplette Besammeln und Quantifizieren des gesamten Größenspektrums der Kolonien einer Art an mehreren sorgfältig ausgewählten Tagen im Verlauf des Jahreszyklus entsteht eine Beschreibung (Soziometrie) von Kolonien bezüglich Wachstum (Soziogenese) und Jahreszeiten (Lebenszyklus im Jahresverlauf). Unser Verständnis der Biologie sozialer Insekten würde durch die breite Annahme der Methode von Soziometrie / Soziogenese als Ausgangspunkt für Studien an sozialen Insekten drastisch verbessert werden.

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